

# FOOD CONSUMPTION, THERMOREGULATION AND ECOLOGY OF THE SKINK *CHALCIDES BEDRIAGAI*

A. HAILEY,\* C. A. ROSE† AND E. PULFORD‡

\* Zoology Department, University of Nottingham NG7 2RD.

† Zoology Department, University of Bristol, Woodland Road, BS8 1UG.  
and

‡ School of Animal Biology, UCNW, Bangor, Gwynedd LL57 2UW.

\* Present address: Department of Physiology, The Medical College of St. Bartholomew's Hospital, Charterhouse Square, London EC1 M 6BQ, UK.

(Accepted 2.6.86)

## ABSTRACT

*Chalcides bedriagai* were found to live under rocks, mostly at body temperatures between 25-35°C, and were active between mid-March and mid-October. Population density (excluding juveniles) was 42 Ha<sup>-1</sup> in an abandoned field habitat, 990 Ha<sup>-1</sup> in the utilised sub-habitat. Larger females had more young (overall range 1-6 per year), but offspring size and relative clutch mass (mean 0.37) were independent of maternal size. Escape success was linearly related to substrate temperature ( $T_s$ ), ranging from 0 at 17°C to 0.5 at 37°C. Pregnant females were found under rocks with higher  $T_s$  than other adults, and had reduced food intake. Food consumption of adults in summer was estimated from the production of urates as 12mg dry weight.g live weight<sup>-1</sup>.day<sup>-1</sup>. This is similar to that of a cool temperate lacertid and a tropical nocturnal gecko, but only half that of a warm temperate lacertid. Energy expenditure on hibernation, maintenance and activity was estimated from the annual temperature profile and values of metabolic rate. Estimates were also made for energy used in reproduction, growth and sloughed skins. The total annual budget suggested an average daily food intake only half of that estimated in summer, and half of that expected from a general relation for active lizards in warm climates.

## INTRODUCTION

Although studies of the thermoregulation of lizards are common, the inconspicuous burrowing and litter dwelling forms have been neglected (Avery, 1982). This is even more true of energetics: despite the evolution of powerful (Nagy and Shoemaker, 1975) and simple (Avery, 1971) techniques of measuring food consumption there are still few data for lizards, and none for burrowing or semi-fossorial (living in litter or under rocks) forms. We took advantage of a convenient population of the semi-fossorial skink *Chalcides bedriagai* to obtain data on these points.

## METHODS

### SITE DESCRIPTION

The study was made in a 3.5 Ha area of abandoned vine fields at Calpe, Spain (41° N, 0° E) from July 1981 to September 1983. The sandy soil was divided into small fields by dry limestone walls, from which rocks had fallen which provided cover for the skinks. The area was completely enclosed, on two sides by hotels, by a major road and by the sea. 1.6 Ha of the area had been spoilt before the study by excavation of sand and

dumping of rocks, possibly as a foundation to building. This spoilage continued during the study, increasing during 1983. The long term prospects for the area, which appeared to be a prime site for hotel development, are doubtful.

The fallen rocks were mostly within 0.5m of the walls, the fields being occupied by old vines, a sparse (less than 5 per cent) cover of grasses and herbs, and a few low shrubs (*Cysticus* and *Thymelea* sp). Reproductive data is included from a few skinks in the nearby Jalon valley; these lizards were larger than those from Calpe.

### THERMOREGULATION

The site was visited in all months from March to October inclusive (in different years), at all times of day. On each visit most of the rocks were turned over (and replaced). They were recorded into the categories large (>30cm greatest dimension), medium (20-30cm) and small (<20cm or <5cm thick). Substrate temperature ( $T_s$ ) was measured in the soil under every rock where a skink was found, and a sample of others from each size category. The skinks were always just under the rocks, sometimes partially buried in the soil but always partly visible. On many occasions we stirred up soil under rocks, but did not locate any skinks in this way.

Body temperatures ( $T_b$ ) were measured by a 0.5mm diameter thermistor probe inserted into the cloaca within 30s of capture.  $T_b$  of juveniles could not be measured. In July 1981 the thermal environment was studied intensively, so that the  $T_s$  under rocks of each size could be described in 1.5 hour periods throughout the day in both sunny and changeable weather (Rose, Pulford and Hailey, MS).

#### ECOLOGY

Lizards were measured snout-vent length SVL and tail length, and weighed with a Pesola scale to 0.1g. They could not be sexed repeatedly, even by probing for hemipenes (females may have a sac in this region, as do *C. ocellatus*; Wilson, 1984), nor could regenerated tails be reliably differentiated from complete ones.

From June to August 1983 all lizards were retained in 10cm plastic petri dishes at room temperature (21–28°C) for seven days, and the faeces and urates produced were collected. The lizards were given water twice during this period. Afterwards those thought to be pregnant were kept in 15 x 10cm sandwich boxes with 2cm of sandy soil at room temperature, and fed on wild crickets until the young were born. Mothers and young were weighed within 12 hours of birth. In view of the site development the skinks were transported elsewhere: this enabled a trap-out density estimate to be made.

#### ENERGETICS

Food consumption was estimated from the production of faeces and urates after Avery (1971). Ten lizards ( $4.7 \pm 1.0$ g (SD)) were kept in 15 x 10cm plastic arenas in a cage heated to 28–30°C by a 60W light for 10 hours a day, falling to 20°C at night. They were fasted for seven days, then fed small mealworms at different constant rates for 14–20 days. The lizards were then kept for seven days at temperatures fluctuating between 20 and 25–28°C, and the faeces and urates produced were collected. This was done three times, with three week intervals of feeding on wild insects in a large cage between trials.

Faeces and urates were dried in a desiccator and weighed to 0.1mg. The faeces produced during and after each of the three feeding trials were pooled, powdered, and the energy content was determined with a Phillipson micro bomb calorimeter (two pellets for each trial). A sample of mealworms were dried at 70°C, powdered, and their energy content determined. Absorption efficiency ((consumption-faeces)/consumption) of energy and of dry weight was calculated for mealworms.

Absorption efficiency was also measured for hard-bodied prey, woodlice. Ten lizards were kept in a 50cm diameter plastic arena, with a lamp for thermoregulation 10 hours a day and folded paper shelters. They were fed woodlice for ten days, uneaten food and faeces being collected daily. Faeces were collected for ten days after feeding. Woodlice and faeces were dried, powdered, and their energy content measured as above.

## RESULTS

#### ECOLOGY

Several trips round the site revealed no lizards in mid-March (1982 and 1983) and late October (1982). Fig. 1 shows the sizes of lizards captured between these periods, with the growth curve estimated from them. Lizards with SVL under 45mm formed a distinct group and were termed juveniles in the field, and it is probable that this size is reached in the July after birth. Lizards of SVL 45–55mm formed a less distinct group, termed subadults; 55mm is probably reached in the second July after birth. Thereafter there were no distinctions, and all were termed adults. Lopez-Jurado, Jordano and Ruiz (1978) recognised four size groups in a field study of this species.

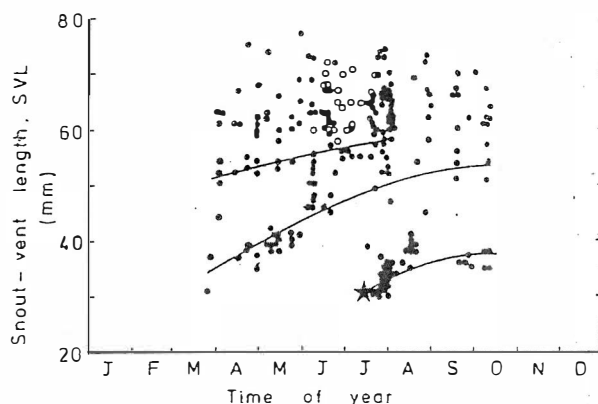


Fig. 1 Sizes of *Chalcides bedriagai* recorded during the annual activity period, with estimated growth curves. The star shows the mean size at, and date of, birth. Open circles are pregnant females.

Without dissection, the only way to distinguish the sexes was in the reproductive season when females were pregnant. Thirty-seven adults were captured in June and before 18 July 1983 (when the first juvenile was seen), and 21 of these later gave birth, suggesting an even sex ratio with breeding every year. Pregnant females had a mean SVL of 68mm, range 57–75mm (two pregnant females from Jalon measured 73 and 84mm).

Offspring size was independent of maternal size (Fig. 2). Mean offspring size was 0.423g (SD = 0.056, correlation with maternal SVL  $r = 0.26$ ,  $n = 47$ ,  $P > 0.05$ ) and 30.4mm (SD = 1.3,  $r = 0.16$ ,  $n = 49$ ,  $P > 0.05$ ). These sizes are similar to those given by Salvador (1981). The number of young increased with maternal size (Fig. 3a), the regression being

Number of young =  $0.114 \text{ SVL (mm)} - 5.2$   
( $n = 22$ ,  $F = 18.7$ ,  $P < 0.001$ ).

The mean number of young was 2.15 per female (2.41 including the two females from Jalon). Relative clutch mass RCM was calculated as total offspring weight/maternal weight after birth (Shine, 1980). This was independent of female size (Fig. 3b);

$$\text{RCM (\%)} = -0.343 \text{ SVL (mm)} + 60$$

(n = 20, F = 0.73, P > 0.5).

Mean RCM was 37 per cent (SD = 11). After birth of the young, females were on average 0.99g lighter than when they were captured, and they produced on average 1.04g of offspring. Thus the females plus young did not increase in weight during the time the female was in captivity. Females ate the placentae after birth. There was no relationship between time in captivity and mean weight of offspring (n = 20, F = 1.2, P > 0.25).

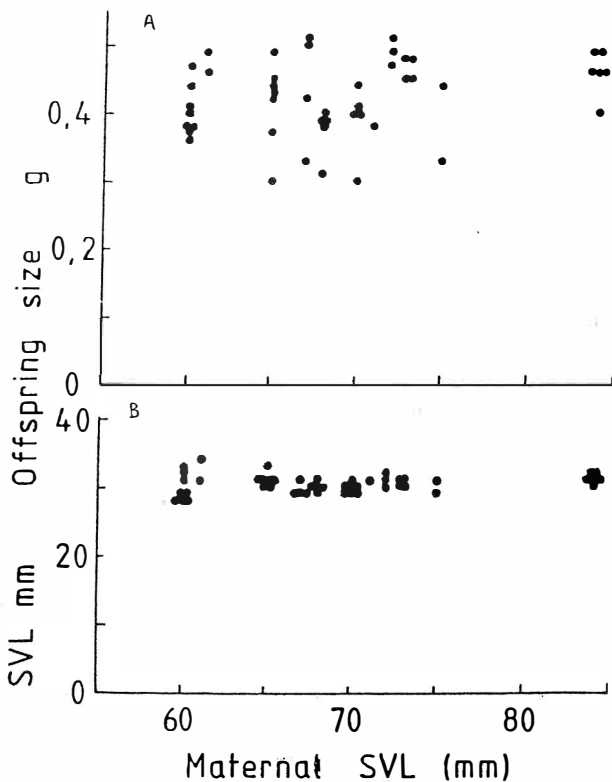


Fig. 2 Independence of (a) offspring weight and (b) offspring length with maternal size.

The trap-out estimate for adults and subadults in this closed population is shown in Fig. 4. This is the intercept of the regression on the abscissa in Fig. 4b (Southwood, 1978), which is 79. This is similar to the minimum population size (the number removed), 77. The crude density (Odum, 1959) was thus 42 lizards  $\text{Ha}^{-1}$  in the undisturbed 1.9 Ha of the site, similar to densities reported for other small skinks (Turner, 1977; Barbault, 1983). The lizards only used the rocks in the areas around the bases of the walls, extending for about 0.5m on each side of the wall. The ecological density (Odum, 1959) was therefore much higher,

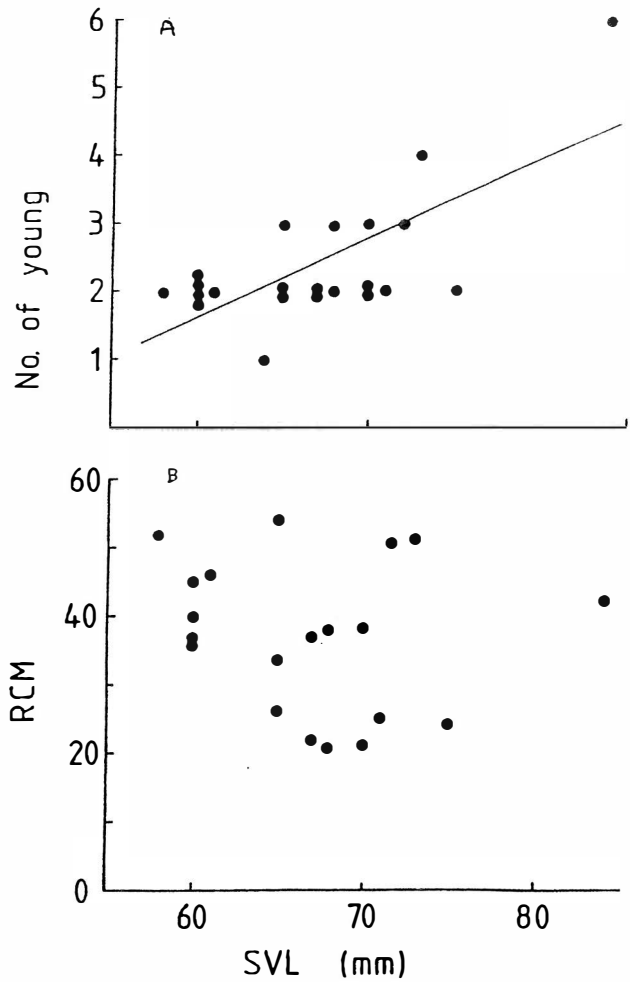


Fig. 3 Relations between maternal size and (a) number of young and (b) relative clutch mass (%).

990  $\text{Ha}^{-1}$  in the 0.08 Ha of their base-of-wall habitat (calculated from an area 0.5m on each side of the wall).

#### ENERGETICS

The weight dependence of production of faeces and urates in the seven days after capture (pregnant females excluded) was described by the equations

$$F = 6.76 W^{1.00 \pm 0.19} \quad (n = 59, r^2 = 0.33, P < 0.01) \quad (1)$$

$$U = 3.98 W^{0.66 \pm 0.13} \quad (n = 59, r^2 = 0.31, P < 0.01) \quad (2)$$

where F and U are dry weights of faeces and urates respectively in mg and W is live weight in g. Hard parts identified in the faeces included the remains of beetles, woodlice, spiders, cockroaches (a small wild species), and orthopterans. The 0.66 exponent for urates is similar to the 0.65 for standard metabolic rate of *C. ocellatus* (Bakker and Andrews, 1984).

Pregnant females produced less faeces and urates than other lizards (Fig. 5). The smallest pregnant female weighed 2.19g; the mean weight-specific production (with SD) of faeces and urates of all lizards of this weight or more was

	Pregnant (n = 21)	Non-pregnant (n = 32)
Faeces $\text{mg.g}^{-1}$	4.1 (2.4)	9.1 (5.6)
Urates $\text{mg.g}^{-0.66}$	2.9 (1.8)	4.7 (2.3)

As the variability increased with the mean in these data, they were log transformed for t tests. The non-pregnant and pregnant means were significantly different for both faeces and urates ( $t = 3.80$  and  $3.18$ ,  $P < 0.001$  and  $P < 0.01$ , respectively).

$F = 0.33 C - 0.9 \quad (n = 30, r^2 = 0.47, P < 0.01) \quad (3)$   
 $U = 0.15 C + 4.5 \quad (n = 30, r^2 = 0.35, P < 0.01) \quad (4)$   
where C is dry weight of mealworms consumed per day (all quantities in mg). The correlation between U and C was not increased by taking account of body weight (i.e. using U expressed as either  $\text{mg.g}^{-1}$  or  $\text{mg.g}^{-0.66}$ , rather than mg), presumably due to the small size range of lizards used in these trials. The dry weight, energy content and absorption efficiencies (AE) of mealworms and woodlice were

	mealworms	woodlice
Dry matter (%)	34	33
Energy (KJ.g dry W <sup>-1</sup> )	23	15
AE energy (%)	92	91
AE dry weight (%)	85	81

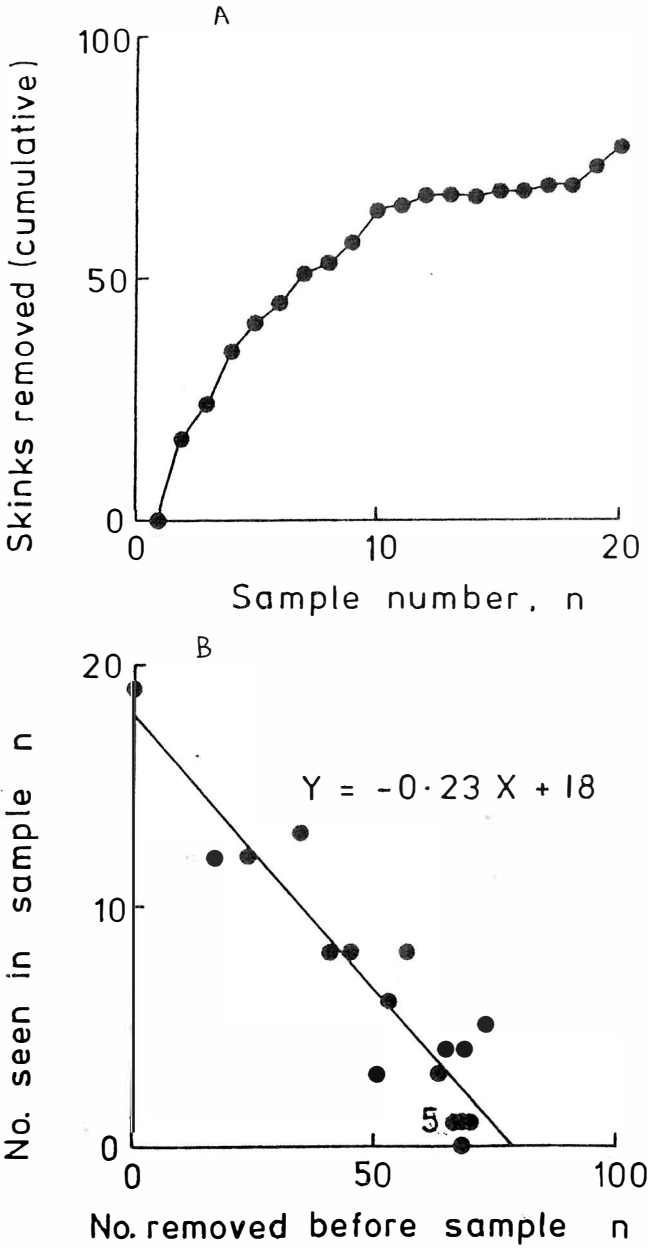


Fig. 4 A trap-out estimate of the total population size of adults and subadults in the study area. (a) The cumulative number of skinks removed in each visit to the site. (b) The relation between the number seen on each visit and the number removed prior to that visit. The regression fit is shown, which estimates the population size as 79 (the intercept on the x axis). The group labelled 5 has five superimposed points.

The production of faeces and urates in seven days after feeding were related to food consumption by the regression equations

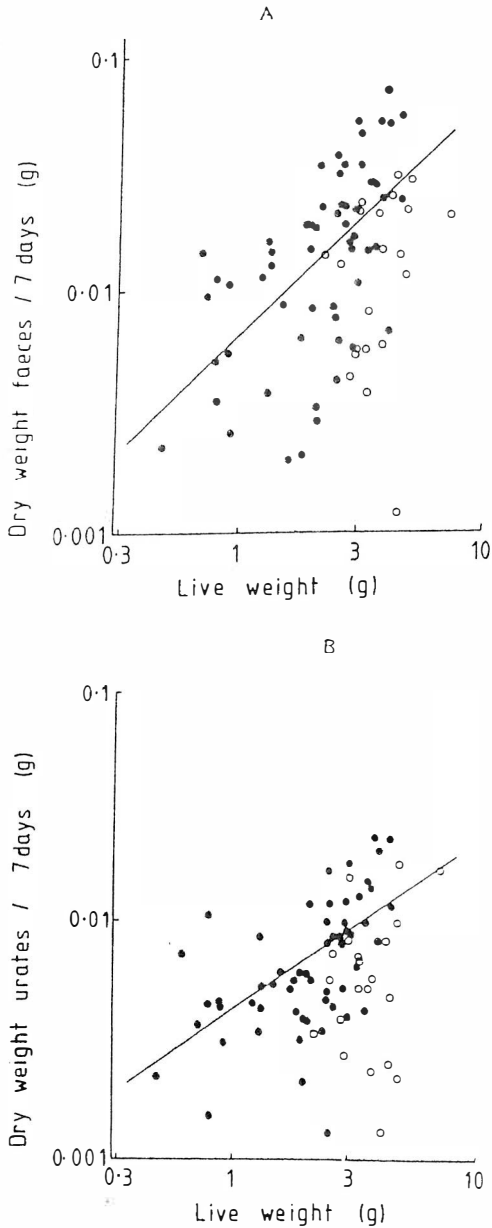


Fig. 5 The relationship between live weight and (a) faeces and (b) urates produced in seven days after capture, all log scales. Open circles are pregnant females. Regression fits (excluding the pregnant lizards) are described in the text.

During one of the feeding trials (a total of about 44 skink-weeks including the FU collection period) eight shed skins were removed from the plastic arenas. This suggests that the lizards shed approximately every 4.5 weeks. Six dried skins had a mean weight of 44mg (SD = 17).

#### THERMOREGULATION

98 per cent of all lizards were found beneath rocks. In addition they may have inhabited the walls themselves. The open areas were too hot to be used in summer ( $T_s > 55^\circ\text{C}$ ), and were always exposed. Bushes covered a very small area compared to the rocks. Body temperatures were similar to the  $T_s$  under the rock from which the lizard came (Fig. 6,  $r = 0.89$ ). The regression of  $T_b$  on  $T_s$  was significantly different from  $T_b = T_s$  (ANCOVA  $P < 0.05$ ), but the differences between  $T_b$  and  $T_s$  were small ( $< 4^\circ\text{C}$ ) and easily attributable to warming in the hand. The small size and overlapping anal scales of this species made rapid measurement of  $T_b$  difficult. As the lizards spent much of the time beneath rocks and at the same temperature as the soil under them, description of under-rock  $T_s$  will provide a good guide to the  $T_b$ s experienced by *C. bedriagai*.

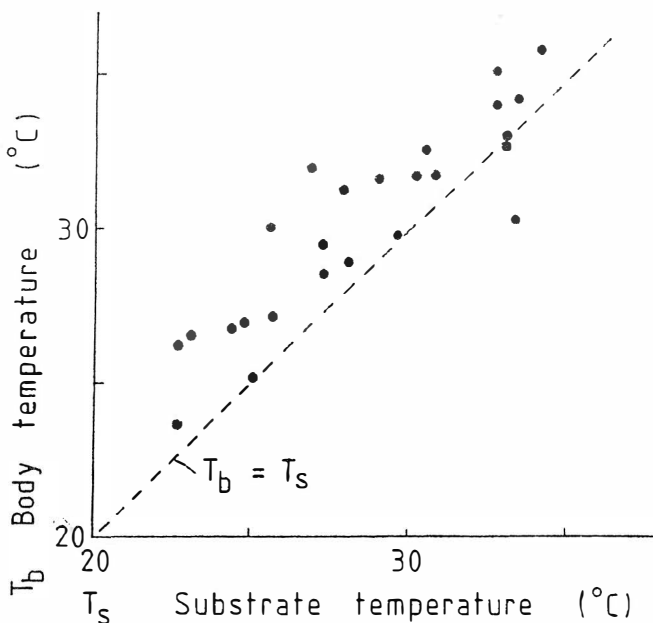


Fig. 6 The relationship between body temperature and the temperature of the substrate under the rock where the lizard was found.

The thermal niche of *C. bedriagai* is shown in Fig. 7. This is the proportion of times spent at different  $T_s$  (and by implication  $T_b$ ), and is used both in the calculation of metabolic costs (below) and in interpretation of temperature-performance relations (Hailey, in prep.) Fig. 7a,b shows  $T_s$  experienced during the night and day, respectively, from data on  $T_s$  at different times of day in each month, and assuming a linear fall in  $T_s$  at night. Substrate temperatures from rocks under which

adult and subadult lizards were found are shown in Fig. 7c. This is a less good measure of their thermal niche during activity, since sampling was not evenly distributed over the yearly and daily activity period. Mean and SD these  $T_s$  are  $28.5$  and  $4.22^\circ\text{C}$  ( $n = 250$ ).

Substrate temperatures selected by pregnant females are compared with those selected by other adults from 7 June to 20 July. Mean  $T_s$  of the pregnant females,  $31.2^\circ\text{C}$ , SD = 3.84,  $n = 21$  was significantly different from that of the other adults,  $28.0^\circ\text{C}$ , SD = 3.20,  $n = 20$  ( $t$  test,  $P < 0.01$ ).  $T_s$  selected by juveniles are compared with those selected by adults and subadults in the period after the birth pulse (5 July to 1 September). There was no significant difference: juveniles mean  $30.2^\circ\text{C}$ , SD = 3.92,  $n = 72$ ; others mean  $29.5^\circ\text{C}$ , SD = 3.57,  $n = 94$  ( $t$  test,  $0.3 > P > 0.2$ ).

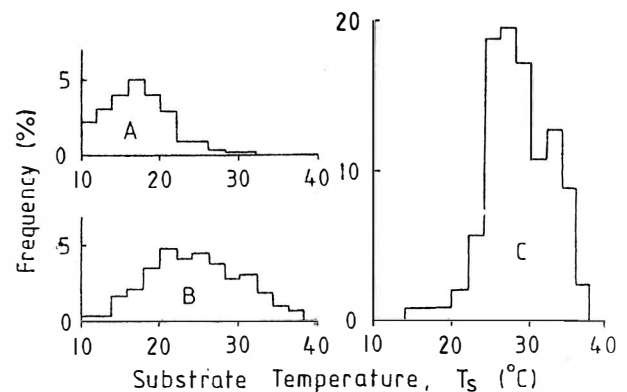


Fig. 7 Frequency distributions of  $T_s$ . (a) Activity season, night. (b) Activity season, day. (c) All rocks under which a lizard was found (all daytime).

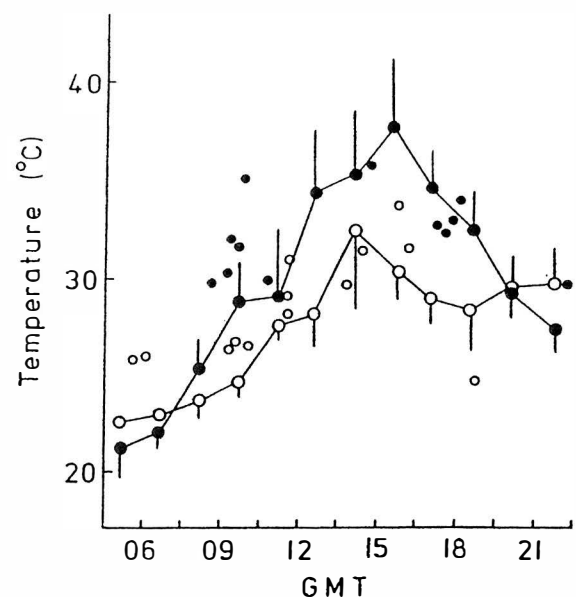


Fig. 8 The effect of weather on environmental and body temperatures at different times of day in July. Dots are for sunny days, open circles for days with broken cloud cover. Small symbols are  $T_b$ s, large joined symbols are mean  $T_s$  (+ or - 1 SD).

Fig. 8 shows the effect of weather on the thermal environment and  $T_b$ s in July. In changeable weather  $T_s$  were significantly lower than on sunny days, and all observed  $T_b$ s were lower than those found at similar times on sunny days. Mean  $T_b$  recorded on sunny July days was  $32.6^\circ\text{C}$ , significantly different from the mean of  $29.1^\circ\text{C}$  for changeable days (F test,  $P < 0.001$ ).

Pregnant females captured early in June gave birth after those captured later in the season, so that the date of birth was dependent on the time that the female had been in captivity (Fig. 9a). This could be an artifact, since females giving birth early could not have been in captivity as long as those giving birth later. The dotted line in Fig. 9a shows the earliest possible birth date for any period in captivity, i.e. points could not occur below this line. The absence of data in this area does not seem responsible for the correlation observed, suggesting that it is a real phenomenon.

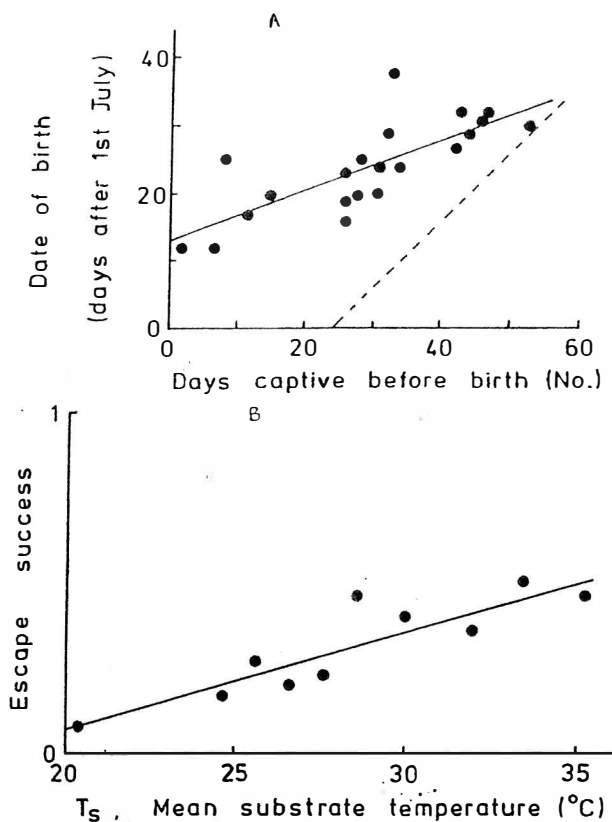


Fig. 9 Two probable thermal effects. (a) Pregnant females held for longer in captivity (at lower  $T_b$  than they would experience in the wild) gave birth at a later date than those held for shorter periods. The dashed line shows the earliest date of birth for each period in captivity. (b) The temperature dependence of escape success. Each point is the mean  $T_s$  and escape success of 25 lizards.

This is probably a thermal effect, since the females were kept at a lower temperature (daytime maximum  $25\text{--}28^\circ\text{C}$ ) than they would have experienced under rocks (mean  $31.2^\circ\text{C}$ ). The regression for the relationship between time in captivity and date of birth (days after 1 July) was:

Date of birth =  $0.37$  days in captivity +  $13$  ( $n = 21$ ,  $F = 26.3$ ,  $P < 0.001$ ). This predicts that the mean birth date in the wild in 1983 was 14 July.

The similarity of  $T_b$  to  $T_s$  allows an unusual opportunity to estimate the  $T_b$  of the lizards that escaped as well as those that were captured. The effect of temperature on escape success (number which escaped/number encountered) can thus be shown in the wild (Fig. 9b). The 250 recorded  $T_s$  for adults and subadults were ranked and divided into ten successive groups: the mean  $T_s$  and escape success were then calculated for each group. The regression fit is

$$\text{Escape success} = 0.029 T_s - 0.50$$

( $n = 10$ ,  $F = 30.1$ ,  $P < 0.001$ ). This predicts that at  $17^\circ\text{C}$  and below all lizards would be captured, and that at the maximum observed  $T_s$  ( $37^\circ\text{C}$ ) about half would escape.

Fig. 10 shows habitat selection in terms of the sizes of rocks occupied at different times of year: lizards preferred larger rocks in summer. The association between rock size and month is significant (September and October combined, G test,  $P < 0.001$ ). This is probably because the soil under the smaller rocks became too hot, although there may have been additional effects of humidity or food investrebrates. On sunny days in July maximum  $T_s$  was reached in the 15.00-16.30 GMT periods: the means ( $^\circ\text{C}$ , with SD) for different rock sizes were

Small	41.0 (1.1)
Medium	38.3 (2.7)
Large	34.0 (2.1)

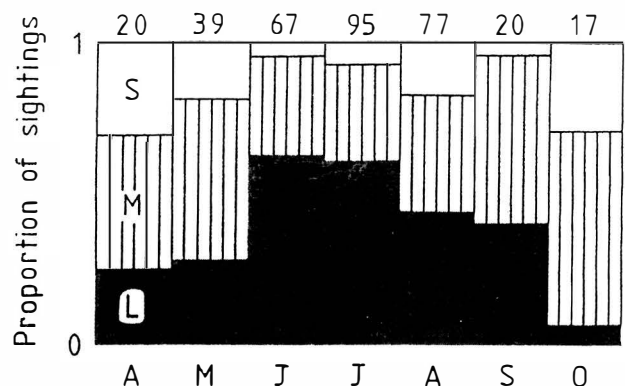


Fig. 10 Habitat selection (small, medium or large rocks) in different months. Numbers show the sample size for each month.

## DISCUSSION

### ECOLOGY AND THERMOREGULATION

The thermal relations observed during July were very similar to those found by Lopez-Jurado, Jordano and Ruiz (1978) in a study of this species on Tabarca Island, Alicante Province. Body temperatures of 72 'active' lizards on Tabarca were in the range  $24\text{--}35^\circ\text{C}$ , mean  $30.5^\circ\text{C}$ ; at Calpe, July  $T_b$ s were in the range  $23.6\text{--}35.8^\circ\text{C}$ , mean  $30.6^\circ\text{C}$ . The mean  $T_s$  of eight refuges was  $28.1^\circ\text{C}$  on Tabarca;  $T_s$  of 125 rocks under which skinks were found at Calpe was  $29.8^\circ\text{C}$  (SD = 3.6).

Lopez-Jurado et al (1978) also noted a close correlation between  $T_b$  and  $T_s$ . This repeatability of results suggests that the thermal relations of *C. bedriagai* have been accurately described.

There is some doubt, however, about the habits of this species and the level of thermoregulation it can achieve. Salvador (1974) suggested that *C. bedriagai* is usually only active in the early morning, when it sets out on a food search, then spends the rest of the day in its hiding place. Lopez-Jurado et al (1978) note that  $T_b$  is greater than  $T_s$  between 06 and 10 h, and that  $T_b$  is independent of air temperature: they suggest that *C. bedriagai* basks in the morning.

Observations at Calpe suggest that this lizard is very seldom active on the surface, and forages under rocks throughout the day. All those disturbed under rocks were alert, rather than sleepy as observed at night in captivity. We found no direct evidence of basking in the field at any time, and attributed the elevation of  $T_b$  above  $T_s$  to warming during measurement. It is possible that skinks select the warmest position under an individual rock. It is admitted, however, that skinks basking near a rock would be inconspicuous and may retire under it before discovery. This type of basking has been seen in *C. ocellatus* (Coborn, 1981), although this species seems to be more active above ground than *C. bedriagai* (Arnold and Burton, 1978). On two occasions a skink from under a cool rock moved faster than it was expected to from previous experience, and this may be evidence for basking. It is unlikely that *C. bedriagai* spend long periods basking in the wild as they will in captivity, but possible thermoregulation must be taken account of in the calculation of metabolic expenditure.

Pregnancy has been found to affect thermoregulation other skinks (Shine, 1980), though as an increase in basking rather than by selection of microclimate. The latter is probably less costly in terms of the time which has to be used thermoregulating, and in the risk of predation. However, another 'cost' of reproduction, reduced food intake, is high in *C. bedriagai* (below).

FOOD CONSUMPTION

Two independent estimates may be made of the food consumption of a 4.7g *C. bedriagai* (the mean size of animals used in the calibration of F and U production) in summer, based on faeces and urate production, respectively. The weight-specific amount of faeces and urates produced by non-pregnant adults, 9.1 mg.g<sup>-1</sup> and 4.7mg.g<sup>-0.66</sup> respectively convert to 43mg faeces and 13mg urates for a 4.7g lizard. These values would be expected from food consumption of 133 and 57mg dry weight. day<sup>-1</sup> from equations 3 and 4, respectively.

Estimates of faeces and urates produced by a 4.7g lizard from equations 1 and 2 (32 and 11mg, respectively) are lower. This is because the regressions are for log-transformed data, in which the effect of the high values is reduced (Sokal and Rohlf, 1981).

Two factors may contribute to the estimate from faeces being higher than that from urates.

- (a) Lizards in the field may ingest sand and dirt with their food, which will pass into the faeces: lizards in clean arenas do not have this problem. This is likely in *C. bedriagai* which lives in sand; Bosca (1880) noted particles of sand in the gut.
- (b) Natural prey may be less easy to digest than mealworms. This may have two effects. Firstly, if the food takes longer to digest, there will be more in the gut at any time. If the gut is evacuated during the seven day period, more faeces will be produced from material with a long passage time. Secondly, if there are hard parts which cannot be digested then more faeces will be produced from a given amount of food (Avery, 1978). This is also likely in *C. bedriagai*, which has previously been found to take at least 50 per cent of prey having hard exoskeletons (beetles) or mineral armour (woodlice) (Table 1). The important measure here is the efficiency of producing faeces, i.e. (100-AE). This was 15 per cent for mealworms and 19 per cent for woodlice on a dry weight basis, which would cause an estimate from faeces to be 25 per cent greater than one from urates.

The value 57mg dry weight.day<sup>-1</sup> from urates is thus preferred. This may be compared to estimates for other lizards using this technique, all calculated for a 4.7g lizard (summer or dry season values, mg dry weight.day<sup>-1</sup>):

<i>Lacerta vivipara</i>	68	(Avery, 1971)
<i>Podarcis muralis</i>	95	(Avery, 1978)
<i>Hemidactylus brookii</i>	46	(Avery, 1981)

Thus food intake of *C. bedriagai* is similar to that of the active cool temperate *L. vivipara* and the tropical nocturnal sit-and-wait *H. brookii*. It is only one half that of the active *P. muralis* from an area of similar climate.

In order to make the estimate of food consumption comparable with a wider range of data for lizards, it may be converted to utilisable energy, using the value 21 KJ.g dry weight<sup>-1</sup> for energy content of small invertebrates and an assimilation efficiency of 90 per cent (Turner, Medica and Kowalewsky, 1976). This gives a 4.7g *C. bedriagai* a utilisable energy intake of 1.08 KJ.day<sup>-1</sup> in summer, similar to the 1.11 KJ.day<sup>-1</sup> calculated for a 4.7g lizard from equation (29) of

	Beetles	Woodlice	Spiders	Other	N
Valverde (1967)	56	19	11	14	73
Mellado et al (1975)	35	22	20	23	40
Seva and Escarre (1976)	47	4	15	34	338

TABLE 1: Published analyses of the diet of *Chalcides bedriagai*. Values are the percentage of N prey items.

Turner et al. (1976). This equation was, however, based on data for average daily intake throughout the active season.

The effect of reproduction on food intake was estimated from the weight-specific production of faeces and urates by pregnant females, 4.1 mg.g<sup>-1</sup> and 2.9 mg.g<sup>-0.66</sup> respectively. These give estimates of food intake of 6l and 24 mg dry weight.day<sup>-1</sup> for a 4.7 g lizard, respectively 46 per cent and 42 per cent of the calculated intake of a non-pregnant lizard of this size.

Part of this reduction might be an artifact of the weight of the young, if these did not contribute to maternal production of faeces or urates. This effect would be greatest if the young were of maximum size, when it would lead to an estimate only 73 per cent (1/1.37) of the real value. The observed reduction is twice as large as this, suggesting that it is real.

ENERGY BUDGET

An estimate of annual energy turnover in an adult *C. bedriagai*, comparable to the data used by Turner et al (1976), may be made from estimates of expenditure on respiration and production.

The cost of respiration is estimated from the body temperature profile and the metabolism-temperature relationship. Values of standard metabolic rate SMR are from Patterson and Davies (1978): over the interval 5-37°C SMR increases exponentially with temperature according to the equation

Log SMR = 0.0431 T + 0.88 (5) (Hailey, in prep.) where SMR is in μlO<sub>2</sub>.g<sup>-1</sup>.h<sup>-1</sup> and T is °C. Over the activity T<sub>b</sub> range 20-37°C active metabolic rate AMR is related to temperature by

Log AMR = 0.0335 T + 1.83 (Hailey, in prep.) giving a mean factorial scope for maximum activity of 4.7 times (range 4.1 at 30°C to 5.9 at 20°C).

The cost of maintenance was estimated from the T<sub>s</sub> profiles in Fig. 7, equation (5), and the conversion 1 ml oxygen consumed = 20 J (Morrison and West, 1975) (Table 2). The frequency distribution of under-rock T<sub>s</sub> in the hibernation period (not shown) was extrapolated from values in October, December and March.

Two estimates were made of the cost of daytime maintenance:

- 1) Using the daytime T<sub>s</sub> profile (Fig. 7b).
- 2) Using the T<sub>s</sub> profile for rocks under which lizards were found (Fig. 7c).

The former is a minimum estimate, and assumes that the lizards do not thermoregulate under any

conditions. The latter is a maximum estimate, and assumes that under any conditions the lizards can reach a preferred body temperature of 25-35°C (distribution 7c is not significantly different from temperatures selected in a thermal gradient — Hailey, in prep.).

Estimating the extra cost of activity depends on the T<sub>b</sub> profile during activity, and the value of routine factorial scope. Three activity T<sub>b</sub> profiles have been used, 1) and 2) as for maintenance above, corresponding to diurnal activity with minimum or maximum thermoregulation, respectively. A third T<sub>b</sub> distribution was added:

- 3) Combining the T<sub>s</sub> profiles of Fig. 7a and 7b, including night T<sub>s</sub> > 20°C and excluding day T<sub>s</sub> < 20°C.

This takes account of the 20°C minimum voluntary temperature for activity (Hailey, in prep.), and includes crepuscular or nocturnal activity where T<sub>s</sub> is high enough.

Routine scope in lizards has been measured as about 2.5-3.5 times SMR during the activity period:

<i>Sceloporus occidentalis</i>	2.5-3.1	(Bennett & Nagy, 1977)
<i>Cnemidophorus murinus</i>	3.4	(Bennett & Gleeson, 1979)
<i>Sceloporus graciosus</i>	3.1	(Congdon & Tinkle, 1982)

Turner et al (1976) used a value of 2.5 in their model; here, following Congdon, Dunham and Tinkle (1982), estimates are given for different values between 1.5 and 3.5 (Table 3). A value in the middle of this range may be most realistic in view of the low scope for maximum activity in *C. bedriagai* (4.7 compared to a mean of about 8 for lizards in general — Kamel and Gatten, 1983).

The cost of producing sloughed skins was estimated as: 0.22 skins per week over a 31 week annual activity period, each skin weighing 44 mg, energy content 23.4 KJ.g<sup>-1</sup>. The latter value is from sloughed snake skins (Smith, 1976). This comes to 7.0 KJ year<sup>-1</sup> for an adult *C. bedriagai*.

The cost of reproduction was estimated from the RCM of 37 per cent and an energy content of the young of 5 KJ.g live weight<sup>-1</sup>, totalling 8.7 KJ.year<sup>-1</sup> for a 4.7 g lizard. In addition there will be a cost associated with development of the young. This may be estimated for the viviparous skink *Sphenomorphus quoyii*, from the chemical composition of the egg and embryo at the start and end of development (Figs. 3d and 5e of

	Hibernation	Night	Day (1)	Day (2)
% of year	41	23	35	35
Mean T <sub>b</sub> (°C)	10.1	17.4	24.4	28.5
Mean SMR (μl.g. <sup>-1</sup> .h <sup>-1</sup> )	21	47	105	146
Maintenance (KJ.year <sup>-1</sup> )	7.3	9.1	30.3	42.1

TABLE 2: Estimates of annual maintenance costs of a 4.7g. *C. bedriagai* from standard metabolic rate and temperature profiles. The two estimates of daytime maintenance (1,2) are from the temperature profiles in Fig. 7b and 7c, respectively (see text).



Thompson, 1981), plus values for the energy content of fat, protein and carbohydrate (Dowgialls, 1975). In *S. quoyii* an average egg contains 7.4 KJ at the start of development, and the offspring contains 5.7 KJ. Thus 1.7 KJ is used during development, 30 per cent of the energy content of the offspring when born. Applying this to *C. bedriagai*, a 4.7g female would spend 2.6 KJ.year<sup>-1</sup> on the young for their development, and their total cost would be 11.3 KJ.year<sup>-1</sup>.

Expenditure on growth of a 4.7g adult lizard may be given minimum and maximum estimates. The former is zero growth, 0 KJ.year<sup>-1</sup>. The latter is that it will grow to the maximum observed size of 6.3g, with the 1.6g of new tissue having an energy content of 5 KJ.g<sup>-1</sup>, giving 8.0 KJ.year<sup>-1</sup>.

These components of the annual energy budget are listed in Table 4, and give an estimate of utilised energy of 81-171 KJ.year<sup>-1</sup> for a 4.7g *C. bedriagai*. This large range mostly results from uncertainty about the annual cost of activity, particularly the value for routine factorial scope; this has much more effect than

differences between differences between temperature profiles (Table 3). In view of the low scope for maximum activity in *C. bedriagai*, a routine scope of about 2.5 seems likely, giving an annual cost of activity of about 52 KJ.year<sup>-1</sup>. Using mean values for the other components, the annual energy utilisation of a 4.7g *C. bedriagai* is 126 KJ.year<sup>-1</sup>.

This energy must be obtained during the 31 week activity period, giving utilisable energy intake of 0.58 KJ.day<sup>-1</sup>. This is only 54 per cent of the estimated 1.08 KJ.day<sup>-1</sup> utilisable food intake in summer, probably reflecting reduced food intake during cool weather, and during pregnancy. 0.58 KJ.day<sup>-1</sup> is 52 per cent of the utilisable intake estimated for a 4.7g lizard from the equation of Turner et al (1976), which is also for average daily intake over the activity season. This data was mostly for lizards of active habits (except *Anolis*, *Sauromalus* and *Egernia*) from warm climates (except *L. vivipara* and *L. agilis*). Thus average daily utilisable energy intake of *C. bedriagai* is only half that expected for an active diurnal lizard from a warm climate.

Temperature profile	Routine factorial scope				
	1.5x	2.0x	2.5x	3.0x	3.5x
1 Daytime T <sub>s</sub>	15	30	45	61	76
2 Observed T <sub>s</sub>	21	42	63	84	105
3 All T <sub>s</sub> >20°C	16	31	47	63	79
Mean	17	34	52	69	87

TABLE 3: Estimates of the annual cost of activity of a 4.7g *C. bedriagai* from different values of routine scope and temperature profiles. Values are KJ.year<sup>-1</sup>.

		KJ.year <sup>-1</sup>	Range	%
Respiration,	Hibernation	7		5
Respiration,	Maintenance, night	9		7
Respiration,	Maintenance, day	36	(30-42)	29
Respiration,	Activity	52	(17-87)	41
Respiration,	Reproduction	3		2
Production,	Skin	7		5
Production,	Reproduction	9		7
Production,	Growth	4	(0-8)	3
Total		126	(81-171)	

TABLE 4: Estimates of annual energy budget components for a 4.7g *C. bedriagai*.

ACKNOWLEDGEMENTS

This work was done during NERC (AH) and SERC (CAR, EP) studentships, with analysis during a NATO/Royal Society ESEP fellowship (AH) at the Zoology Dept., University of Thessaloniki, Greece, made possible by the kind provision of facilities by

Prof. M. E. Kattoulas and Dr. N. S. Loumbourdis. We also thank Drs. P. M. C. Davies (locating the site, discussion), R. A. Avery (thermistor, discussion) and Maria Lazaridou — Dimitriadis (bomb calorimeter). A preliminary account of fieldwork in July 1981 was given by Rose et al (MS).

## REFERENCES

- Arnold, E. N. and Burton, J. A. (1978). *A field guide to the reptiles and amphibians of Britain and Europe* London, Collins.
- Avery, R. A. (1971). Estimates of food consumption in the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* **40**, 351-366.
- Avery, R. A. (1978). Activity patterns, thermoregulation and food consumption in two sympatric lizard species from central Italy. *Journal of Animal Ecology* **47**, 143-158.
- Avery, R. A. (1981). Feeding ecology of the nocturnal gecko *Hemidactylus brookii* in Ghana. *Amphibia-Reptilia* **1**, 269-276.
- Avery, R. A. (1982). Field studies of body temperatures and thermoregulation. In *Biology of the Reptilia* **12**, 93-166. Gans, C. and Pough, F. H. (Eds). London and New York, Academic Press.
- Bakker, A. M. and Andrews, R. M. (1984). Intraspecific allometry of standard metabolic rate of *Chalcides ocellatus*. *Journal of Herpetology* **18**, 85-86.
- Barbault, R. (1983). Reptiles in Savanna ecosystems. In *Tropical Savannas*, Ed. F. Bourliere, 325-336. Amsterdam, Elsevier.
- Bennett, A. F. and Nagy, K. A. (1977). Energy expenditure in free-ranging lizards. *Ecology* **58**, 697-700.
- Bennett, A. F. and Gleeson, T. T. (1979). Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus*. *Copeia* **1979**, 573-577.
- Bosca, E. (1880). *Gongylus bedriagai*, nueva subespecie de la peninsula iberica. *Annals Soci. Espanola Hist. Nat. Madrid* **9**, 495-503.
- Coborn, J. (1981). Notes on the ocellated skink *Chalcides ocellatus* *ililigugu*. *ASRA Journal* **1**(2), 15-23.
- Congdon, J. D., Dunham, A. E. and Tinkle, D. W. (1982). Energy budgets and life histories of reptiles. In *Biology of the Reptilia* **13**, 233-271. (Ed). C. Gans and F. H. Pough, London, Academic Press.
- Congdon, J. D. and Tinkle, D. W. (1982). Energy expenditure in free-ranging sagebrush lizards (*Sceloporus graciosus*). *Canadian Journal of Zoology* **60**, 1412-1416.
- Dowgialls, A. (1975). Chemical composition of an animal's body and of its food. In *Methods for Ecological Bioenergetics*, 160-185. Eds. Grodzinski, W., Kekowski, R. Z. and Duncan, A. (IBP Handbook No. 24) Oxford, Blackwell.
- Kamel, S. and Gatten, R. E. (1983). Aerobic and anaerobic activity metabolism of limbless and fossorial reptiles. *Physiological Zoology* **56**, 419-429.
- Lopez-Jurado, L. F., Jordano, P. and Ruiz, M. (1978). Ecologia de una poblacion insular mediterranea del eslizon iberico *Chalcides bedriagai*. *Donana, Acta Vertebrata (Seville)* **5**, 19-34.
- Mellado, J., Amores, F., Parreno, F. F. and Hiraldo, F. (1975). The structure of a Mediterranean lizard community. *Donana, Acta Vertebrata (Seville)* **2**, 145-160.
- Morrison, P. and West, G. C. (1975). Methods of measuring respiratory exchange in terrestrial vertebrates. In *Methods for Ecological Bioenergetics*, 293-300. Eds. Grodzinski, W., Kekowski, R. Z. and Duncan, A. (IBP Handbook No. 24), Oxford, Blackwell.
- Nagy, K. A. and Shoemaker, V. (1975). Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiological Zoology* **40**, 252-262.
- Odum, E. (1959). *Fundamentals of Ecology*. Philadelphia, W. B. Saunders.
- Patterson, J. W. and Davies, P. M. C. (1978). Thermal acclimation in temperate lizards. *Nature, London* **275**, 646-647.
- Rose, C. A., Pulford, E. and Hailey, A. (MS) Thermo-regulation, habitat selection and ecology of the skink *Chalcides bedriagai* in Eastern Spain. (Presented at the International Herpetological Congress, Oxford, October 1981).
- Salvador, A. (1974). *Guia de los anfibios y reptiles españoles*. Madrid, ICONA.
- Salvador, A. (1981). *Chalcides bedriagai*: Iberischer Walzenskink. 309-317. In *Handbuch der Reptilien und Amphibien Europas I*. Ed. W. Bohme. Wiesbaden, Akademische Verlag.
- Seva, E. and Escarre, A. (1976). El eslizon iberico (*Chalcides bedriagai*) en el medio insular de Nueva Tabarca (Provincia de Alicante). *Mediterranea, Alicante* **1**, 61-115.
- Shine, R. (1981). 'Costs' of reproduction in reptiles. *Oecologia (Berlin)* **49**, 92-100.
- Smith, G. C. (1976). Ecological energetics of three species of ectothermic vertebrates. *Ecology* **57**, 252-264.
- Sokal, R. R. and Rohlf, F. J. (1981). *Biometry*. (2nd Ed.). San Francisco, Freeman.
- Southwood, T. R. E. (1981). *Ecological Methods* (2nd Ed.) London, Chapman and Hall.
- Thompson, J. (1981). A study of the sources of nutrients for embryonic development in a viviparous lizard, *Sphenomorphus quoyii*. *Comparative Biochemistry and Physiology* **70A**, 509-518.
- Turner, F. B. (1977). The dynamics of populations of squamates, crocodilians and rhynchocephalians. In *Biology of the Reptilia* **7**, 157-264. Eds. Gans, C. and Tinkle, D. W. London, Academic Press.
- Turner, F. B., Medica, P. A. and Kowalewsky, B. W. (1976). Energy utilisation by a desert lizard (*Uta stansburiana*). *US/IBP Desert Biome Monograph* (1). Utah State University Press, Logan.
- Valverde, J. A. (1967). Estructura de una comunidad mediterranea de vertebrados terrestres. *Mon. Cienc. Mod. Madrid (CISC)*. 1-218.
- Wilson, I. B. (1984). Work on lizards in the School of Animal Biology, UCNW, Bangor. *Bulletin of the British Herpetological Society* (9), 13-15.